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Electroantennogram responses of the Mediterranean fruit fly, *Ceratitis capitata*, to the volatile constituents of nectarines

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Abstract

Electroantennograms (EAGs) were recorded from laboratory-reared, male and female *Ceratitis capitata* (medfly) in response to individual volatiles identified from ripe nectarines. Uniformity in EAG response between the sexes was observed for most test compounds. Only 10 volatiles, of the 44 nectarine volatiles tested, elicited significantly different EAG responses between the sexes. No correlation was observed between the magnitude of antennal responsiveness and the concentration of a particular volatile in the headspace odor of ripe nectarines. The most abundant ('major') nectarine volatiles were among the least EAG stimulatory compounds tested. And certain 'minor' and 'trace' volatiles were the most potent compounds in eliciting EAGs. Moreover, the magnitude of antennal response to a nectarine volatile was related to the functional-group, chain-length, and unsaturation of the compound. The degree of potency of the compounds was as follows: six-carbon unsaturated aldehydes and alcohols ≥ methyl and ethyl hexanoates and octanoates ≥ hexenyl acetates and monoterpenes > shorter chain-length acetates and alcohols > lactones. Unsaturated aldehydes, alcohols, and acetates generally elicited larger EAGs than their saturated analogs, with the (E)-2-isomers being the most potent isomeric configurations. In addition, medfly antennae exhibited 'long recovery' periods (i.e., > 10 sec.) for the EAG tracings to return to baseline potential after stimulations with certain classes of compounds, *e.g.*, C_6 to C_8 acid esters, monoterpenes, and hexen-1-ols. The potential adaptiveness to medflies for selective sensitivity to these volatiles is discussed.

Introduction

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (medfly) is a polyphagous, world-wide pest, attacking 253 known fruits, nuts and vegetables; with 40 of these hosts being categorized as 'heavily or generally infested' (Hagen *et al.*, 1981, Liquido *et al.*, 1990). Thirteen of these 40 highly-susceptible fruit hosts are found in temperate areas, with the stonefruits (apricots, cherries, nectarines, peaches and plums) the most representative species group. In 1918, Back and Pemberton stated that, 'the peach (*Prunus persica*) is the most preferred of all hosts fruits grown in

Hawaii and in other countries', with nectarines (*P. persica nectarina*), apricots (*P. armieca*), and plum species (*e.g., P. domestica* and *P. salicina*) also reported as 'well-infested'. Medfly preference for, and/or host susceptibility of peaches, nectarines, and apricots, and to a lesser degree plums, has been demonstrated in recent Hawaiian field sampling studies of differential infestation, pupation, and adult emergence (Wong *et al.*, 1983, Nishida *et al.*, 1985; Liquido *et al.*, 1990).

Host searching behavior of medflies and most tephridis is dependent on both olfactory and visual cues (Prokopy, 1986; Prokopy & Roitberg, 1984). Medflies are known to be attracted to complex botanical extracts from various host and non-host plants and various individual plant volatiles (Beroza & Green, 1963; Keiser *et al.*, 1975). Further, female medflies are preferentially attracted to the aroma of ripening fruits (including peaches and nectarines) over the aromas of under-ripe fruits (Light & Jang, in preparation; Jang *et al.*, unpublished) or over-ripe and fermented fruit (*e.g.*, peaches; Vita *et al.*, 1986). Recently, Levinson *et al.* (1990) demonstrated a differential antennal receptivity of medflies to essential oils of apricots and three citrus host fruits. Three recent electroantennogram (EAG) studies showed that medflies were differentially receptive to specific, straight-chain aliphatic alcohols, aldehydes, acids, and acetates; which include general leaf and fruit volatiles (Guerin *et al.*, 1983; Light *et al.*, 1988; Bigiani *et al.*, 1989). However, no experiments have been undertaken on medflies to systematically assess the selectivity of their chemoreception of the chemically-defined volatiles of a particular host fruit.

Volatiles of nectarines were chosen for our investigations because nectarines, a subspecies of peaches, are one of the highly-preferred hosts of medflies and the identity of many volatiles of intact nectarines have been determined (Takeoka *et al.*, 1988). The purpose of this initial study was to investigate, by means of EAG recordings, the peripheral olfactory selectivity of adult *C. capitata* to the principal components of the headspace aroma of intact, ripe nectarines.

Material and methods

Insects. Pupae of *C. capitata* were obtained from a laboratory colony maintained at the USDA, Tropical Fruit and Vegetable Research Laboratory, Honolulu, Hawaii. Upon arrival, pupae were segregated as to their sex and placed in separate cages. Emergent adults were provided sucrose, hydrolyzed protein, and water until they were tested two to five days after emergence.

Olfactory stimuli. Table 1 lists the 44 compounds tested, their purities, supply sources, and their reported percent concentrations in concentrates prepared from nectarines and other stonefruits. Among the 44 compounds tested were the 35 principal constituents identified from the headspace of intact, ripe nectarines (Takeoka *et al.*, 1988). Combined, these 35 constituents account for nearly 95 percent of the total gas chromatographic (GC) peak area of the nectarine headspace components. Nine additional components (hexenals, hexenols, and *gamma* and *delta* lactones) were tested, due to their previous identification from ether extractions of blended nectarine tissue (Engel *et al.*, 1988a).

The test compounds were dissolved in spectrometric grade hexane (treated with Ionox antioxidant) to form 10% volume solutions (i.e., approx. 100 $\mu g/\mu l$ solutions). From these solutions, 1 μl aliquots (approx. 100 μg of test odorant) were pipetted onto glass-fiber filter papers, solvent was allowed to evaporate for ca. 30 sec, then the filter papers were inserted into Pasteur pipette cartridges. Each test cartridge was loaded within a minute of its presentation to the antenna.

EAG technique. EAG deflections were recorded, measured, and stored on a Nicolet 4094 digital oscilloscope in the manner previously described (Light *et al.*, 1988). The antennae were continuously bathed in a stream of charcoal-filtered, humidified air. A 'puff' of a test compound was delivered to the antennae when a three-way solenoid valve was activated, diverting air through the test cartridge for a 1 sec stimulation interval. To insure full recovery of the antennal receptors, a 3 min purge period of air preceded and followed each compound stimulation. For each compound tested, EAGs were recorded from at least five flies of each sex. 'Control' stimuli (1 μl of hexane solvent) and 'standard' stimuli (1 μl of 1% hexan-1-ol in hexane or ca. a 10 μg dose) were interspersed about every fifth compound tested. EAG responses (mV) to a test compound were first adjusted by substraction of response to accompanying 'control' and then expressed as percent response to the 'standard'. Mean responses were compared using the nonparametric Mann-Whitney U test. Only relative comparisons can be made between the odorous stimuli because of the inherent broad range in volatility of the nectarine components tested.

Results

In general, significant differences in magnitude of the medfly antennal responses were observed for the nectarine odor components. These differences appear to be related to the functional-group classification of the compound and the particular chain-length and/or molecular configuration of the compound. Although slight response differences in EAG amplitude to each test compound were found between the sexes, for only ten of the 44 components tested were the differences significant ($P \leq 0.05$). The mean EAG responses of male and female medfly antennae were virtually identical for both the hexane 'control' (females, $X = -0.38$ mV ± 0.05 mV SE; males, -0.45 ± 0.04 mV) and hexan-1-ol 'standard' (females, -0.75 ± 0.06 mV; males -0.72 ± 0.05 mV).

Selectivity to nectarine volatiles

Major and intermediate headspace constituents. All three of the 'major' constituents (*i.e.*, most abundant, >7% total GC area) of the nectarine headspace (ethanol, ethyl acetate, and methyl acetate) elicited relatively low EAG responses (*i.e.*, <75% of response to standard) in medflies (Fig. 1, Table 1). Of the four 'intermediate' constituents (*i.e.*, moderately abundant, between 2 and 1% of total GC area), three [methyl octanoate, (Z)-3-hexenyl acetate, and ethyl octanoate] evoked moderate amplitude EAG responses, and one (propan-2-ol) elicited low amplitude EAGs (Fig. 1). Female EAG responses were significantly greater than male responses for both ethyl acetate ($P \leq 0.01$) and methyl octanoate ($P \leq 0.03$).

Minor headspace constituents. The 'minor' constituents (each ranging from 0.5 to 0.01% total GC area) as a class had a combined GC peak area of only 4.05 percent of the total headspace area for the ripe nectarine odor. But these 'minor' volatiles consisted of 33 components , of which 22 were tested (Table 1). Overall, the 'minor' components were moderately to highly stimulatory to medfly antennae (Fig. 1). Relatively large amplitude EAGs (*i.e.*, >160% of response to standard) were elicited by ethyl hexanoate, hexanal, 3-methylbutyl acetate, and methyl heptanoate, while moderate amplitude EAGs were recorded in response to a number of esters (ethyl butyrate, hexyl acetate, and pentyl acetate), alcohols [(Z)-3-hexen-1-ol, hexan-1-ol, and pentan-3-ol], and monoterpenes (limonene, myrcene, *gamma*-terpinene, (E)-*beta*-ocimene, linalool, *beta*-phellandrene, and *p*-cymene). EAG responses of female medflies were significantly greater ($P \leq 0.05$) than those of males for (Z)-3-hexen-1-ol, ethyl butyrate, hexanal, and myrcene; while males were more responsive than females only for stimulations by *beta*-phellandrene.

Trace headspace constituents. Arbitrarily only 6 of the 42 'trace' components (each <0.01% GC area) of the nectarine headspace were tested. Of all the headspace volatiles tested, the 'trace' constituent, (E)-2-hexen-1-ol, elicited the largest EAG responses from medfly antennae (Fig. 1). The remaining 'trace' constituents that were tested elicited only low EAG responses, except for moderate responses to 3-methylbut-2-enyl acetate and octyl acetate.

Non-headspace constituents. The nine additional nectarine pulp volatiles tested are fundamental to human olfactory discrimination of stonefruit

Table 1. Source, purity and the medfly EAG selectivity ranking of volatiles of ripe nectarine and their percent or categorical presence in the analyzed odors of ripe nectarines, other ripe stonefruits, and the complex pheromonal odor of calling male medflies

Constituents	Sample chemical purity (%)[a]	Source[b]	Presence in nectarines			Presence in other stonefruits					Presence in male medfly odor[k]	Ranking of EAG selectivity[l] ♀:♂
			Intact[c]	Blended[d]	Pulp[e]	Peach	Plum		Apricot			
						f	g	h	i	j		
Aldehydes												
Hexanal	98	A	0.01%	0.91%	24.44%				0.01%	5.8%		6:8
(E)-2-Hexenal	99	A		4.70	49.50					19.2		1:1
Benzaldehyde	99	A	tr*	2.33	0.25	M	0.03%	tr		1.5	tr	35:35
Alcohols												
Ethanol	100	B	57.44			m	4.69	M	M	M	m	42·42
Propan-2-ol	99	C	1.04									44:43
2-Methylpropan-1-ol	99	D	0.06				2.44	I			tr	30:30
Pentan-3-ol	98	E	0.14	0.03								23:16
Hexan-1-ol	98	A	0.02	27.52	2.26	I	47.02	I	0.31	19.5		18:25
(E)-2-Hexen-1-ol	97	A	tr	24.64	2.13	I		m		19.8		3:3
(Z)-2-Hexen-1-ol	94	A		0.01								4:4
(Z)-3-Hexen-1-ol	98	A	0.21	9.97	1.38			I		1.5		10:21
(E)-3-Hexen-1-ol	98	A		0.15				tr				13:18
Esters												
Methyl acetate	80	F	7.21	0.09		I					tr	37:39
Ethyl acetate	99	G	22.38	2.51		M		M	M	M	M	32:37
Propyl acetate	98	H	0.16	0.06				tr			m	33:29
2-Methylpropyl acetate	96	E	0.27	0.09				tr				29:31
Butyl acetate	98	E	0.01	tr				M	0.42		tr	31:27
3-Methylbutyl acetate	64	H	0.19	0.04			2.25	tr			tr	8:6
3-Methylbut-2-enyl acetate	92	I	tr								tr	11:11
Pentyl acetate	99	D	0.05	0.02		tr		tr	0.02			24:24
Hexyl acetate	93	A	0.25	1.32	0.25	I	1.26	M	0.15		tr	20:20
(E)-2-Hexenyl acetate	95	J		0.63	0.13	I				0.4		2:2
(Z)-3-Hexenyl acetate	98	K	1.89	3.77	0.63	M		I				15·12
Octyl acetate	98	D	tr									21:23
Ethyl butyrate	99	E	0.05					tr	2.00		tr	17:28
Ethyl hexanoate	98	G	0.12				0.52	m	4.70	tr	tr	5:6
Methyl heptanoate	98	F	0.03									9:10
Methyl octanoate	95	L	1.08	0.03					0.01			7:9
Ethyl octanoate	99	A	1.84	0.01			0.07	m	0.01			16:17

Monoterpenoids												
Myrcene	65	I	0.51								I	12:19
Limonene	92	M	0.25			I			0.03		tr	14:7
(E)-β-Ocimene	86	I	0.26						0.06	0.1	I	22·13
Linalool	97	N	0.34	2.91	6.27	M	3.83	tr	0.11	7.8	I	25·26
p-Cymene	90	E	0.05								tr	26 22
β-Phellandrene	80	O	0.05		<0.10							27:15
γ-Terpinene	83	D	0.02		0.38						tr	19:14
α-pinene	80	N	tr									28:32
Lactones												
γ-Hexalactone	98	P	0.07	1.40	3.38	I		m			tr	34·34
γ-Heptalactone	88	L		0.13	0.13	m						40·33
γ-Octalactone	95	A	tr	0.41	0.13	I		m	0.06	0.2		38:36
γ-Nonalactone	89	Q		0.05	<0.10	m	0.07	m				43:40
γ-Decalactone	97	A		9.85	2.76	D	0.13	I	1 83	13.0		39:38
δ-Decalactone	95	R		2.24	2.38	M			0.07	1.1		36·44
γ-Dodecalactone	97	K		0.23	<0.10	m			0.10	1.5		41 41

[a] Capillary GLC analysis (12 5 m × 0.2 mm methyl silicone cross-linked column, DB-1).

[b] A, Aldrich Chemical Co.; B, U.S. Industrial Chemicals Inc.; C, Baker Chemical Co.; D, source presently unknown, from file at USDA-ARS-WRRC; E, Eastman Kodak Co.; F, Supelco Inc.; G, Alltech Inc.; H, Chem Supply Co.; I, sample from R. G. Buttery, USDA-ARS-WRRC; J, CTC Organics; K, Tokyo Kasei; L, K & K Laboratories; M, Fluka Chemical Co.; N, sample from L Light, USDA-ARS-WRRC; O, sample from K. L. Stevens, USDA-ARS-WRRC; P, sample from R. A. Flath, USDA-ARS-WRRC; Q, Norda Chemical Co.; R, sample from G. R. Takeoka, U. C. Davis.

[c] Takeoka *et al*, 1988: Tenax trapping of headspace constituents of intact, tree-ripened nectarines (of the 116 components identified, 34 were tested here; which account for 94.92% of the GC headspace area).

[d] Takeoka *et al*, 1988. vacuum steam distillation of blended ripe nectarines (of the 63 components identified, 18 were tested here; which account for 77.97% of distillate's GC area).

[e] Engel *et al.*, 1988a: liquid-liquid ether extraction of blended ripe nectarine pulp (of 33 components identified, 19 were tested here; which account for ca. 98 36% of the extracts GC μg/kg fruit pulp).

[f] Spencer *et al.*, 1978: steam distillation of skinned peach halves (15 of the 24 components identified were tested here).

[g] Ismail *et al.*, 1981: Porapak Q trapping of headspace constituents of intact, fully-ripe plums (*P. domestica*) (of the 38 peaks, 33 components were identified and 11 were tested here; which account for 62.31% of the GC headspace area).

[h] Forrey & Flath, 1974: sliced ripe Santa Rosa plums (*P. salicina*) were vacuum co-distilled with water followed by diethyl ether extraction (18 of the 53 components identified were tested here, including 4 of the 5 major components, 5 of the 6 intermediate components, and 6 of the 14 minor components).

[i] Takeoka *et al.*, 1990· Tenax trapping of headspace constituents of intact, tree-ripened apricots (of the 86 components identified, 18 were tested here; which account for 10–14% of the GC headspace area).

[j] Takeoka *et al.*, 1990: Vacuum steam distillation of blended ripe apricots (of the 49 components identified, 16 were tested here; which account for 91.4% of the GC headspace area).

[k] Jang *et al.*, 1989a: Tenax trapping of the headspace constituents of 'calling' virgin male medflies (of the 69 peaks, 58 components were identified, 24 of which are also constituents of the intact nectarine headspace and 19 of those were tested here).

[l] Rankings of the relative EAG percent response magnitude from highest (No. 1) to lowest (No. 44) for the 44 compounds tested at doses of ca. 100 μg.

* Components: D, dominant; M, major; I, intermediate; m, minor; tr, trace.

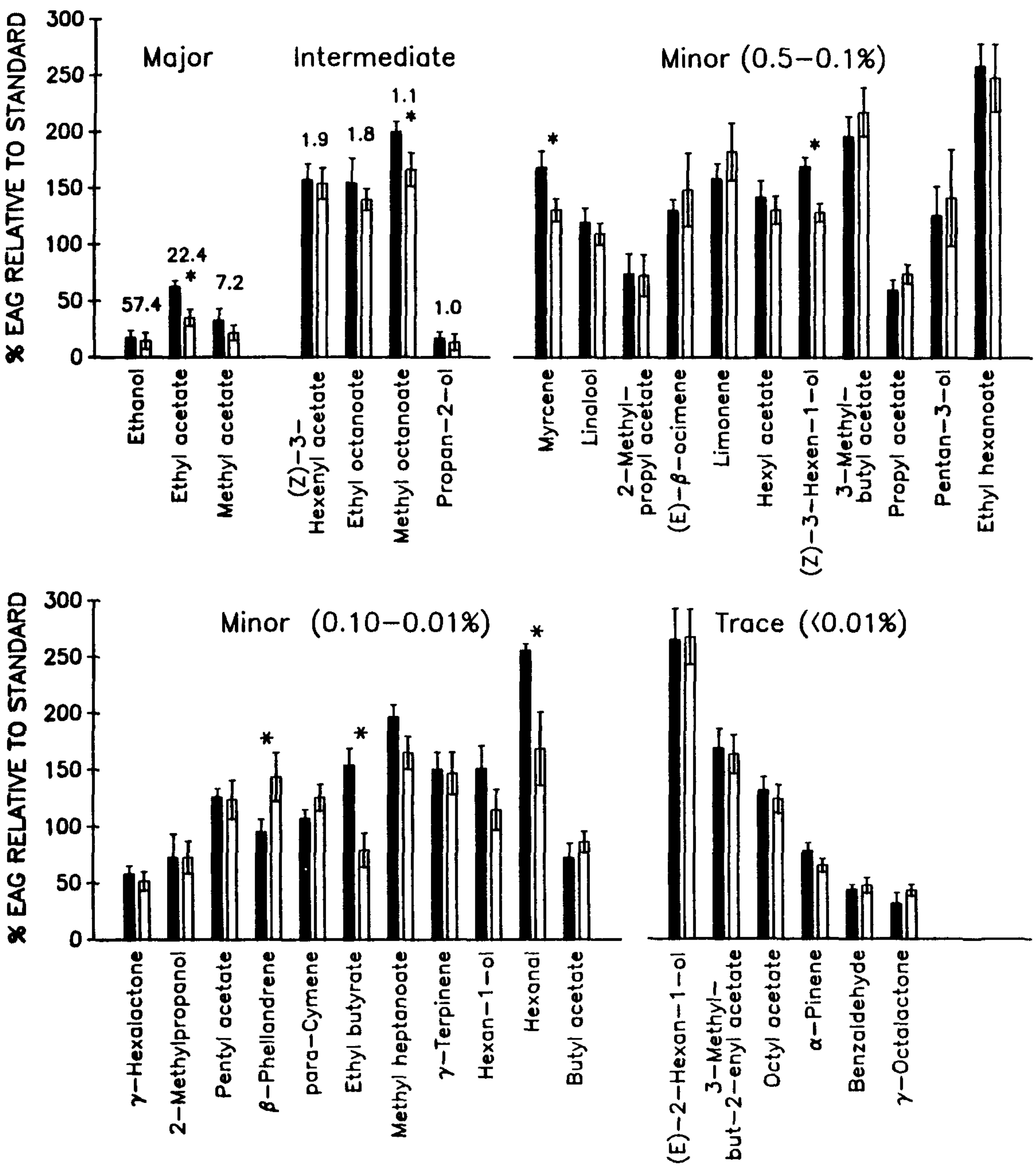

Fig 1. Mean EAG responses of female (solid bars) and male (blank bars) *C. capitata* to 1 μl doses of 10% solutions (ca. 100 μg of compound) of the 'major' and 'intermediate' components, 'minor' components (ranging from 0.5 to 0.1 and 0.1 to 0.01 percent concentration), and 'trace' components (<0.01 percent concentration) of the headspace aroma of intact nectarines. The numbers above the bars for the major and intermediate components represent the analyzed percent concentration of that component in the headspace aroma. Vertical lines represent standard errors, n = five, a 100% response is approx. 0.73 mV, and an asterisk represents a significant difference in responsiveness between the sexes to that component.

aroma. These volatiles were isolated from steam distillation and liquid-liquid extractions of pureed nectarines and identified as a series of lactones and six-carbon aldehydes, alcohols and acetates (Engel *et al.*, 1988a; Takeoka *et al.*, 1988). If present in the headspace of intact ripe fruit, these volatiles are at levels below the detection limits of the particular trapping/analysis sequences that have been employed (Takeoka *et al.*, 1988).

The six-carbon components, that are dominant volatiles of green, unripe nectarine pulp (Engel *et al.*, 1988b), elicited the largest EAGs of all the nectarine compounds tested on medflies (Fig. 2, Table 1). Generally, for these C_6 compounds larger EAGs were elicited by, 1) unsaturated than saturated molecules, 2) unsaturation at the second-carbon position than at the third-carbon position, and 3) aldehyde than alcohol or acetate functional-groups. Female antennae were significantly more responsive than male antennae to hexanal, (E)-3-hexen-1-ol, and (Z)-3-hexen-1-ol.

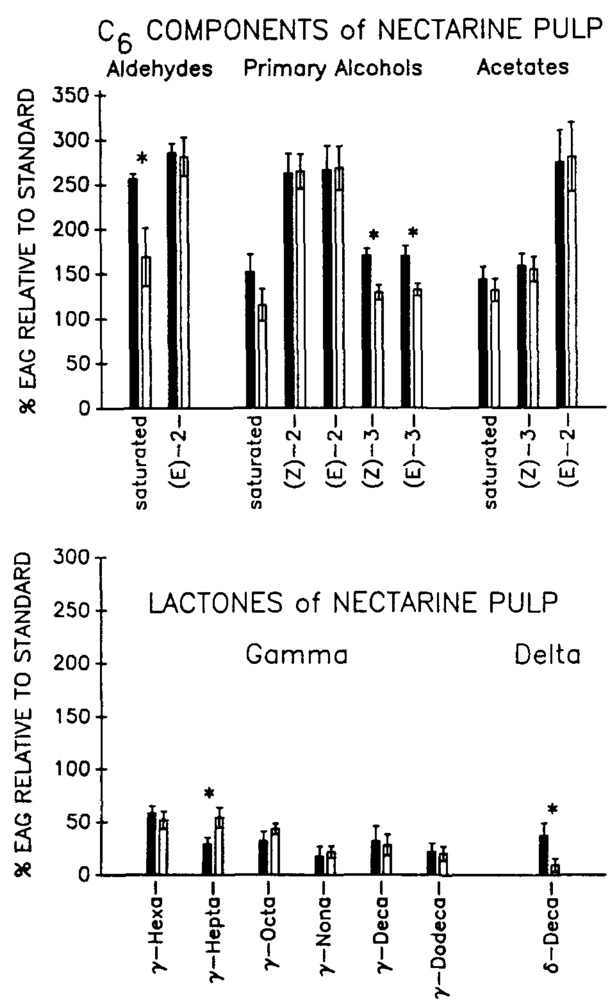

Fig. 2. Mean EAG responses of female (solid bars) and male (blank bars) *C. capitata* to 1 μl doses of 10% solutions (ca. 100 μg of compound) of the saturated and unsaturated six-carbon aldehydes, primary alcohols and acetates, and also the *gamma*- and *delta*-lactones present in a liquid-extraction concentrate of blended nectarine pulp. See Figure 1 for further information.

The EAG responses of medflies to the series of lactones were generally the lowest in amplitude of all the tested compounds. However, this might partially be due to the lactones as a group having generally the lowest volatility of the compounds tested. Females were significantly more responsive to *delta*-decalactone than males, while the reverse was found for *gamma*-heptalactone (Fig. 6).

Recovery period

An unusually 'long recovery' period for the EAG trace to return to baseline potential was observed only after presentation of certain classes of compounds (*e.g.*, functional-group, chain-length, and position and type of geometric isomerism) and in many cases the same compounds that elicited the largest EAG response amplitudes. The recovery period of the EAG trace was classified as 'normal' if the deflection trace returned to the approximate baseline potential within three seconds of the termination of the stimulus. 'Long recovery' stimulations did not return to baseline potential within the field of view of the oscilloscope screen (ca. 10 sec), with certain compounds eliciting prolonged recoveries of up to three minutes. 'Slightly long recovery' stimulations were classified as those that returned to baseline within the three to ten second viewing time.

Generally, 'long recovery' periods occurred when the medfly antennae were stimulated by: 1) longer chain-length esters, either C_6, C_7, and C_8 acid esters or C_6 acetates, 2) monoterpenes, and 3) hexen-1-ols (Table 2). All stimulation replications of ethyl octanoate elicited 'long recoveries', while fewer recordings of a 'long recovery' nature were observed with stimulations by ethyl hexanoate, methyl octanoate, and methyl heptanoate. Also, (E)-2-hexenyl acetate, *gamma*-terpinene and limonene elicited a greater number of record-

Table 2. Number of medfly EAG recordings in which nectarine volatiles elicited 'slightly long recovery' or 'long recovery' periods*

	Females		Males		Combined percent occurrence in recordings
	Slightly long	Long	Slightly long	Long	
Aldehydes					
Hexanal		1			10%
Benzaldehyde		1		1	20%
Alcohols					
Ethanol	1				10%
Pentan-3-ol	2				20%
Hexan-1-ol				1	10%
(*E*)-2-Hexen-1-ol	1	2		1	40%
(*Z*)-3-Hexen-1-ol		2			20%
(*E*)-3-Hexen-1-ol	1				10%
Esters					
2-Methylpropyl acetate	1				10%
Hexyl acetate			2		20%
(*E*)-2-Hexenyl acetate	3	1	1	3	80%
(*Z*)-3-Hexenyl acetate		1	1	1	30%
Ethyl hexanoate		5		3	80%
Methyl heptanoate	2	1	2	1	60%
Methyl octanoate	1	3	1	2	70%
Ethyl octanoate		5		5	100%
Monoterpenes					
Mycrene		5		1	60%
(*E*)-*beta*-Ocimene	1	2		2	50%
beta-Phellandrene		2	1	1	40%
p-Cymene	1	1	2	1	50%
Limonene	1	4	2	1	80%
gamma-Terpinene	1	4		4	90%
Totals:	15	41	12	28	

* A total of five recordings for each sex were made, see Results for definitions of recovery periods.

ings exhibiting 'long recovery' periods than other analog compounds. Replicate stimulations of female medfly antennae tended to exhibit a more frequent occurrence of 'long recovery' responses than male antennae, especially for alcohol compounds (Table 2).

Discussion

Aroma composition of nectarines

Presently, the least intrusive method for examination of the aroma profile released by intact ripe fruit is by headspace-adsorptive-trapping followed by GC-MS analysis, as has recently been conducted on plums (Ismail *et al.*, 1981), nectarines (Takeoka *et al.*, 1988), and apricots (Takeoka *et al.*, 1990); but not to date on peaches (Straten & Maarse, 1983) (Table 1). The more traditional approaches of steam distillation and solvent extraction of fruit pulp produce considerable qualitative and quantitative changes ('distortions') in the fruit odor profile, largely as a result of tissue disruption followed by enzymatic and/or thermal processes. It is apparent from Table 1 that intact stonefruits (nectarines, plums, and apricots) present a different overall ripe-fruit aroma than pureed fruits. Qualitative and quantitative differences in chemical composition reported in such parallel studies of a given fruit are primarily due to fruit treatment differences (intact vs. blended tissue), choice of concentration method (headspace trapping vs.steam distillation extraction vs. direct solvent extraction), sample selection (variation between fruit varieties), and detection and identification limitations of a given analytical approach. With these precautions expressed, the headspace analysis of intact ripe nectarines shows that its aroma is dominated (ca. 87%) by the simple and highly volatile constituents, ethanol and ethyl and methyl acetates, followed by much lower concentrations of other esters (ca. 6.0%), monoterpenes (ca. 1.5%) and alcohols (ca. 1.5%) (Table 1).In comparison, the steam distillation and liquid extraction analyses of blended nectarines identified predominantly six-carbon aldehydes and alcohols (ca. 68–80%), followed by lactones (ca. 9–14%), monoterpenes (ca. 3–7%), and acetates (ca. 1–9%).

Ethyl acetate and ethanol were reported to be 'major' components of concentrates prepared from varieties of each of the four listed stonefruits (Table 1). Both of these compounds are ubiquitous ripening products of fruits in general (Buttery, 1981; Straten & Maarse, 1983). Distinguishing principal volatiles of these stonefruits are: for peaches, benzaldehyde, (Z)-3-hexenyl acetate, linalool, limonene, and *gamma*- and *delta*-decalactone; for plums, hexan-1-ol, hexyl acetate and butyl acetate; and for apricots, hexan-1-ol, (E)-2-hexen-1-ol, ethyl hexanoate, ethyl butyrate, linalool and *gamma* decalactone (Table 1). Thus, the most common, though not necessarily characteristic, volatiles of these four stonefruits are: ethyl acetate, ethanol, hexan-1-ol, linalool, and *gamma*-decalactone.

Antennal selectivity to nectarine volatiles

Headspace composition vs. EAG potency. Figures 1 and 2 illustrate that medfly antennae are responsive to all the volatile constituents tested. However, medfly antennae appear to be selective in the magnitude of their EAG response to particular compounds and to classes of compounds. For example, EAG responses were low to the 'major' headspace volatiles of nectarines and high to certain of the 'intermediate' and 'minor' concentration constituents. Thus, there is no apparent relationship between the contribution, (*i.e.*, relative concentration) that a particular volatile component gives to the aroma of stonefruits (*e.g.*, any of the 'major' components) and the EAG response magnitude (*i.e.* the relative size of the population of responding receptors). The low EAG responsiveness to the 'major' volatiles of nectarines (ethanol, ethyl acetate, and methyl acetate) by medfly antennae may reflect a general lower number of receptors responsive to highly volatile, low molecular weight compounds (four carbon atoms or less) that was previously reported (Light *et al.*, 1988). However, this appears to be contrary to the recent EAG data of Bigiani *et al.* (1989); where medfly antennae exhibited a response ranking of butanol > pentanol > hexanol > ethanol > hexanal. The potency of larger molecules, as we report, may be based on the molecule's chain-length, functional-group, and unsaturation (Light *et al.*, 1988; Jang *et al.*, 1989a). Thereby, medflies may discriminate between, for example, their highly-preferred stonefruits (peaches and nectarines) and their less-preferred stonefruits (*e.g.*, plums) by assessing the overall chemical blends of the aromas. A peripheral olfactory receptivity to a broad range of fruit volatiles with a central integrative network in the brain that 'views' the mosaic of input responses by the diverse receptor populations ('across-fiber processing') may enable the medfly to reach a discrimination of different fruit aromas (Light, 1986; De Jong & Visser, 1988; Visser & De Jong, 1988).

The potency of specific chain-lengths, functional-groups, and unsaturation are evident when the 20 compounds eliciting the greatest EAG responses of female medfly antennae are ranked in the following hierarchy: (E)-2-hexenal ≥ (E)-2-hexenyl acetate ≥ (E)-2-hexen-1-ol ≥ (Z)-2-hexen-1-ol ≥ ethyl hexanoate ≥ hexanal > methyl octanoate ≥ 3-methylbutyl acetate = methyl heptanoate > (Z)-3-hexen-1-ol $\geq$ 3-methylbut-2-enyl acetate = myrcene = (E)-3-hexen-1-ol > limonene $\geq$ (Z)-3-hexenyl acetate $\geq$ ethyl octanoate = ethyl butyrate $\geq$ hexan-1-ol = *gamma*-terpinene > hexyl acetate (Table 1). This EAG activity ranking also provides clear proof that EAG responsiveness is not due to the dramatic differences in vapor pressure of the test molecules (or stimulant quantity) but is based on the molecules' chemical structures (or stimulant quality). The only appreciable difference between the above ranking for females and that of males is that for males there is, 1) a general increase in responsiveness to the monoterpenes, limonene, (E)-*beta*-ocimene, *gamma*-terpinene, and *beta*-phellandrene and 2) a lower responsiveness to myrcene, (Z)-3-hexen-1-ol, hexan-1-ol, and ethyl butyrate (Table 1). This EAG potency ranking has obvious clusterings of classes of structurally similar compounds, with the most potent being the C_6 unsaturated alcohols and aldehydes, C_6 to C_8 acid esters, hexenyl acetates, and monoterpenes; and the least potent being the lactones and shorter chain-length acetates (Table 1).

Green leaf volatiles. Molecules having a six-carbon chain moiety dominate the above medfly EAG potency hierarchy of the nectarine volatiles. All of the top six and 11 of the top 20 compounds possess a C_6 structure or substructure. The most potent C_6 components were unsaturated at the 2-position and of the (E) geometric configuration. Aldehydes exceeded alcohols and acetates in their potency. The C_6 compounds tested are common plant volatiles. Further, six of the C_6 alcohols and aldehydes are botanically ubiquitous, frequently contributing to or dominating the odor composition of intact or damaged green leaves and green, unripe fruit of most plants. This blend of ubiquitous volatiles, termed the 'general green-leaf volatiles' (GLVs), is composed of: hexanal, (E)-2-hexenal, (Z)-3-hexenal, hexan-1-ol, (E)-2-hexen-1-ol, and (Z)-3-hexen-1-ol (Visser *et al.*, 1979; Buttery, 1981).

The qualitative and quantitative composition of the GLVs varies between different plant species and as a result of damage to plant tissue. Because these GLVs are commonly produced through enzymatic breakdown of linoleic and linolenic acids, damage to plant leaf parenchyma or fruit tissue (e.g., by herbivory) can greatly enhance this breakdown (Visser *et al.*, 1979; Buttery, 1981).

Maturation of plants, especially fruits, effects the qualitative and quantitative compositional contribution of GLVs to plant aromas. The GLVs represent only a minor contribution to the aroma of ripe, fully-mature nectarines and stonefruits (Table 1). However, when nectarines are immature (viz. green in color) the GLVs comprise the main aroma components, at a level ca. nine times that found in the pulp of fully-mature, tree-ripe nectarines (Engel *et al.*, 1988b). The work of Engel *et al.* (1988b) shows that the ratios of these components can significantly change during the ripening of nectarines. In their study, concentrations of (E)-2-hexenal and (E)-2-hexen-1-ol in ripening nectarines dropped at rates of two to seven times that of the other major component, hexanal. Thus, quantitative and qualitative chemical analyses of GLVs can indicate either the maturation state of a stonefruit or the degree of plant damage incurred by a stonefruit.

The selective and keen EAG receptivity to the GLVs by medflies (Light *et al.*, 1988), oriental fruit flies (Light & Jang, 1987), and many other diverse insects species (see for review, Visser, 1983, 1986; Light *et al.*, 1988) indicates that their antennae possess large populations of GLV-responsive acceptor/receptors which, in concert with other sensory stimuli (*e.g.*, olfactory, visual, and tactile), would provide a degree of discrimination potentially utilized in adaptively avoiding inappropriate resources, *e.g.*, under-ripe fruit and/or damaged fruit (Light & Jang, 1988. Jang & Light, unpublished). For example, significant olfactory-based preferences to alight and oviposit on ripening, softened fruits than immature, green, hard fruits (*e.g.*, papayas, stonefruits, etc.) has been demonstrated for both gravid female medflies (Light & Jang, 1988) and oriental fruit flies (Jang & Light, 1991). Damage to fruit tissues resulting from ovipositional punctures or feeding activity by flies or maggots, would enhance the release of the GLVs. This, in turn, could signal foraging females that the fruit has already been exploited as an ovipositional site. In flight-tunnel bioassays, Light and Jang (1988; in preparation) observed that gravid female medflies will more readily and to a greater extent alight upon, spend time on, and oviposit within artificial fruit models (7.5 cm diam., perforated, yellow polyethylene spheres; McInnis, 1989) that emanated the headspace aroma of ripe nectarines than identical fruit models emanating both the ripe nectarine aroma and synthetic GLVs. Thus, the normal attraction, arrestant, and oviposition behaviors stimulated by the odor of ripe nectarines was disrupted by 'mimicking' the aroma of immature or damaged fruit through the artificial increase in the quantitative levels of GLVs. Similarly, Vita *et al.* (1986) found that the normal attraction of female medflies to purees of ripe peaches was disrupted by much larger amounts (10% w/w and greater) of either ethanol or methanol, which 'mimic' an over-ripe, fermented fruit condition.

Esters. Some of the most potent components tested, besides the GLVs, were the esters, specifically the ethyl and methyl esters of C_6 to C_8 acids and the hexenyl acetates. Other esters, *i.e.* shorter chain-length acetates, were significantly lower in EAG potency. Some general selectivity and potency trends were apparent in the series of esters tested: 1) ethyl esters > acetates (ethyl hexanoate > hexyl acetate), 2) unsaturated acetates > saturated acetates [(E)-2-hexenyl acetate > hexyl acetate], 3) position and geometric configuration in unsaturated compounds [(E)-2- > (Z)-3-hexenyl acetate], 4) the chain-length of the alcohol moiety of the esters (methyl > ethyl octanoate), 5) the chain-length of acetate esters ($C_6 > C_8 \geq C_5 > C_4 > C_3 = C_2 > C_1$), and 6) the chain-length of the acid moiety of the ethyl esters ($C_6 > C_8 \geq C_4$). An indication of the biological significance of medflies' EAG sensitivity to these esters has been suggested by Light and Jang (1988; in preparation). They found that by supplementing the natural, ripe nectarine headspace aroma with the simple methyl and ethyl octanoates and hexanoates caused the attraction, arrestment, and oviposition responses of gravid female medflies to be synergistically enhanced to more than double their responses to ripe nectarine aroma alone.

Sexuality. There was a high degree of response uniformity between the sexes. Only 10 of the 44 nectarine volatiles tested elicited significantly different EAG responses between the sexes. Eight nectarine constituents (one 'major', one 'intermediate', four 'minor', and two 'pulp volatiles') elicited greater EAGs in female than male antennae, while male response was greater for only two constituents. Recently, Levinson *et al.* (1990) found sexual dimorphism in EAG (*ie.* 'receptor potentials') responses of medflies, with female responsiveness greater than males to the complex odors of citrus and apricot essential oils. However, similarity between the sexes in EAG responses to individual volatiles of plants is commonly reported for tephritids, *e.g.*, the apple maggot (Fein *et al.*, 1982), olive fruit fly (Van der Pers *et al.*, 1984), oriental fruit fly (Light & Jang, 1987), and medflies (Light *et al.*, 1988; Jang *et al.*, 1989a; Bigiani *et al.*, 1989). This similarity between the sexes in magnitude and selectivity of EAG responses to various fruit and leaf odors suggests that receptivity to the same plant odors might be adaptive for both sexes.

Medfly females forage for appropriate fruit (*e.g.*, host vs. nonhosts) of suitable quality (*e.g.*, ripe vs. under- or over-ripe) (Back & Pemberton, 1918; Wong *et al.*, 1983; Nishida *et al.*, 1985; Vita *et al.*, 1986). Olfactory chemoreception by gravid female medflies is suggested to be fundamental for these discriminations, based on prior reports of selective foraging for host fruits to oviposit within (Prokopy & Roitberg, 1984; Vita *et al.*, 1986; Papaj *et al.*, 1989; Prokopy *et al.*, 1989; Jang & Light, unpublished). Furthermore, male medflies have been observed to occasionally forage for and reside on host fruits upon which they switch from a lek mating strategy to ambushing, courting, and/or 'raping' ovipositing females (Prokopy & Hendrichs, 1979; Burk & Calkins, 1983; Prokopy & Roitberg, 1984).

Recovery period

The occurrence of a 'long recovery' period following antennal stimulations of medflies by certain of the most potent EAG stimulants (the long-chain esters, monoterpenes, and hexen-1-ols) may be due to a strong interaction (viz., 'high affinity' of these molecules with their acceptors (Roelofs, personal communication), or due to a slow 'inactivation' of the ligand odor-molecule with its acceptors, carrier-molecule(s), or degradative complexes (Kaissling, 1986; Vogt & Riddiford, 1986). Recently, long EAG recovery periods were elicited when particular isomers of trimedlure (those attractive to medflies) were presented to medfly antennae (Jang *et al.*, 1989b). Antennae of the oriental fruit moth (Roelofs *et al.*, 1969) and other insects (Roelofs, personal communication) show longer EAG recovery periods when stimulated with attractive pheromone components than analog or other compounds that are less behaviorally attractive or non-attractive. 'Long recovery' periods have also been elicited in EAG recordings of other tephritid species, *e.g.* when apple maggot antennae are stimulated by various long chain-length apple esters (Ann Averill, personal communication) that are behaviorally attractive (Fein *et al.*, 1982).

Relationships to behavioral activity

We are presently investigating whether nectarine volatiles that elicit either long EAG recovery periods (the long chain-length esters, monoterpenes, and hexen-1-ols) or large amplitude EAGs will also stimulate attraction, repulsion, deterrence, or other behavior modifying properties in medflies.

Also, potential parsimonious bioactivity of certain blends of compounds common to both the aroma of a preferred host fruit (*e.g.*, nectarines) and the pheromonal odor of calling male medflies (Jang *et al.*, 1989a) (Table 1) is under investigation. These commonly shared compounds might contribute to the attractive and/or aggregative properties of their complex original odors. The odor of calling male medflies was found to be comprised of 58 identified components (Jang *et al.*, 1989a), of which nearly half (*i.e.* 24) are shared constituents with the nectarine headspace aroma.

In addition to influences on the selection of appropriate host fruit, the GLVs might have semiochemical influences on medfly mating behaviors, in: 1) the selection of lek calling sites by males, 2) the calling behavior of the males, 3) the release of pheromone, and/or 4) the impact or context of the pheromone message as received by females. These conjectures are based on the observations that: 1) males seek out lek sites on both host and non-host plants, 2) males establish individual lek territories on and call from leaves, 3) females land on leaves upon which they are courted and mated, and 4) the excision of antennae (the principal olfactory organ) disrupts mating (Féron, 1962; Nakagawa *et al.*, 1973; Prokopy & Hendrichs 1979; Burk & Calkins, 1983; Prokopy & Roitberg, 1984; Arita & Kaneshiro, 1985). Therefore, since the GLVs are an olfactory environmental attribute of the leaf substrate upon which medfly reproductive behaviors are performed, we tested in dual-choice, flight tunnel bioassays the ability of GLVs to modulate the attraction of female medflies to the natural odor of calling males. We found that GLVs indeed do, in this context, enhance the attractancy of the natural medfly pheromone and female medflies prefer pheromone with GLVs over pheromone alone (Dickens *et al.*, 1990; Light & Jang, in preparation).

Thus, medfly antennae apparently possess a broad array of populations of olfactory receptors responsive to components of a complex host fruit aroma, such as that of nectarines. However, the largest populations of these olfactory receptors were responsive to the GLVs. The enhanced olfactory capability for detection of the green-leaf volatiles may have parsimonious, multifunctional, and context-dependent effects in, for example, aiding medflies in their discrimination of 1) their host fruit's 'ripeness' or ovipositional resource quality and 2) perhaps more subtly their selection of lek sites and mates.

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